Permian–Triassic evolution of the Bivalvia: extinction-recovery patterns linked to ecologic and taxonomic selectivity

Chenyi Tu[1], Zhong-Qiang Chen[1, *], David A.T. Harper[2]

[1]State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (Wuhan), Wuhan 430074, China

[2]Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham DH1 3LE, UK

*Corresponding author (ZQC): e-mail: zhong.qiang.chen@cug.edu.cn

Abstract

The Bivalvia is an important benthic clade that was relatively less affected than other benthos during the Permian–Triassic (P–Tr) biotic crisis, reporting losses of 85%, 64%, and 32% at the species, genus and family levels, respectively. This clade proliferated immediately after the P–Tr mass extinction (PTME) to become one of the key elements of the 'Modern Evolutionary Fauna' following the P–Tr 'Great Dying'. Global bivalve occurrence data demonstrate that the initial recovery started in the Griesbachian, a substage immediately after the PTME, and are characterized by relatively high origination and low extinction rates. Thus, unlike other fossil groups, bivalves did not significantly engage in the survival interval. The initial Griesbachian recovery is followed by a stepwise recovery during the Dienerian to Spathian. Then, a remarkably rapid radiation occurred in the Anisian, indicated by extremely high proportional origination and extinction rates. Infaunalization has long been considered the most significant adaptation during the Mesozoic Marine Revolution (MMR), which was thought to have commenced in the Early–Middle Triassic. However, the proportion of infauna in communities remained virtually unchanged before and after the P–Tr biotic crisis; additionally there was no significant difference inproportional extinction/origination rates between infaunal and epifaunal taxa at the genus and family levels through the entire P–Tr transition, implying the absence of ecological

selectivity, a conclusion that differs from some previous studies. Therefore, if escalating predatory pressure indeed played a crucial role in driving the initial phases of the MMR, infaunalization was not marked prior to the Ladinian. Alternatively, infaunalization may have played a minor role in facilitating the MMR during the entire era. If so, changes in the physical and chemical environment ('Court Jester' model) (i.e. amelioration of marine environments in late Early Triassic), rather than biotic processes ('Red Queen' model), may be crucial for the origination and initial phases of the MMR during the early Mesozoic.

Keywords: mass extinction; biotic recovery; infaunalization; Mesozoic Marine Revolution; macroevolution

1. Introduction

Of the 'Big Five' mass extinctions, the Permian–Triassic (P–Tr) biotic crisis resulted in the largest drop in biodiversity and the most devastating ecosystem collapse during the Phanerozoic (Sepkoski, 1981, 1984). Global biodiversity data show that various fossil groups behaved differently during and after the PTME. Some clades like brachiopods and corals that suffered substantially during the biotic crisis recovered much later than some other groups (Hallam and Wignall, 1997; Erwin, 1998; Chen et al., 2005a, b); others such as ammonoids (Brayard et al., 2009), foraminiferans (Song et al., 2011), and ophiuroid echinoderms (Chen and McNamara, 2006) rebounded earlier after the P–Tr crisis. The distinctive responses to the PTME and its aftermath may be due to the different roles that various clades played within the trophic structure of the marine ecosystem (Chen and Benton, 2012). The biotic groups within the low-level trophic structure may have garnered relatively less attention from the PTME, and thus rebounded earlier than the meso-consumers or predators (Chen and Benton, 2012). Alternatively, physiologic adaptation in some key groups may have developed resistance to environmental devastation such as widespread anoxia, ocean acidification, and extreme hot seawater temperatures (Knoll

et al., 2007; Payne and Clapham, 2012); such resistance may be accountable for the biodiversity variations within the various groups over the P–Tr transition. Thus, both the physiology and ecological function of organisms provide some clues for unraveling the causes of the PTME and its protracted recovery (Knoll et al., 2007). Nevertheless, to date, debate still continues on whether the physical and chemical environment ('Court Jester' model) or biotic processes ('Red Queen' model) have driven biotic macroevolution over this critical interval (Benton, 2009; Chen and Benton, 2012).

Like many other clades, the Bivalvia underwent its greatest macroevolutionary turnover during the P–Tr transition (Erwin, 1994, 2006; Hallam and Wignall, 1997). They were subordinate in Permian communities, but became the most numerically abundant shelly fossils in the Griesbachian, the first substage following the PTME. Bivalves, together with other molluscs (i.e. ammonoids and gastropods), successfully usurped brachiopod dominance in marine shelly communities through the P–Tr transition (Thayer, 1985; Fraiser and Bottjer, 2007; Chen et al., 2010). This is possibly because they are less sensitive to anoxia (Taylor and Brand, 1975; Bayne and Livingstone, 1977; Wang and Widdows, 1993a, b; Diaz and Rosenberg, 1995; Sobral and Widdows, 1997; MacDonald et al., 1998; Ballanti et al., 2012).

Another feature of the PTME is the switch from brachiopod-dominated Paleozoic Evolutionary Fauna (EF) to mollusc-dominated Modern EF in marine ecosystems (Gould and Calloway, 1980; Sepkoski, 1981, 1984; Bambach et al., 2002; Fraiser and Bottjer, 2007; Alroy, 2010; Chen et al., 2010). The marine ecosystem has undergone an unprecedented, far-reaching transformation in the aftermath of the PTME that is mainly responsible for the marine ecosystem we have today. The term "restructuring" is more appropriate than "rebound" or "recovery" to describe the turnover in the biosphere (Dineen et al., 2014).

Previous studies show that the Bivalvia only suffered moderate disruption during the PTME based on variation in taxonomic richness and extinction rates (Nakazawa and Runnegar, 1973; Yin, 1985, 1987; Li, 1995; Fang, 2004; Huang et al., 2014). They underwent a gradual and stepwise recovery after the PTME (McRoberts,

2001). However, these observations were based mainly on changes in taxonomic richness without consideration of other important proxies, like proportional extinction and origination rates, as well as ecological selectivity through this critical interval. The updated, global database for the bivalves mitigates sampling bias and Lazarus effects that would largely obscure the real changing pattern of biodiversity. In addition, bivalve lifestyles are categorized into five types: infaunal motile, infaunal slow-moving, semi-infaunal motile, epifaunal stationary and low-level epifaunal stationary modes (Li, 1995; Komatsu et al., 2008; Huang et al., 2014). They represent various physiologic types associated with different habitats and climatic regimes. The proportional extinction and origination rates of the various physiologic groups may provide some insight into the environmental and climatic extremes associated with the PTME and subsequent events.

Infaunalization was supposedly prevalent amongst Early Mesozoic bivalves (McRoberts, 2001) by the fact that the proportion of the infauna was higher, possibly much higher than that of the epifauna (Vermeij, 1977; Thayer, 1979). Although the origination rates of the epifauna and infauna showed no significant differences, the epifauna had much higher extinction rates than that of the infauna during the same interval (McRoberts, 2001). Here, we probe the extinction and recovery patterns of the Bivalvia and their ecologic selectivity over the P–Tr transition by re-examining the global dataset derived from the Paleobiology Database with emphasis on the variations in taxonomic richness, and proportional extinction and origination rates at the species, genus and family levels, respectively. Infaunalization through the entire Early Triassic is also assessed on the basis of proportions of infauna/epifauna in the aftermath of the PTME, testing the possible driving force of the MMR in the early Mesozoic.

2. Materials and methods

All bivalve occurrences from the Changhsingian (highest Permian), Lower Triassic substages to the Anisian (Middle Triassic) analyzed in this study are sourced

from Paleobiology Database [*http://fossilworks.org/bridge.pl? a=displayBasic DownloadForm*] and were downloaded in May, 2014. To enhance the resolution of the geological timescale, the Induan and Olenekian were subdivided into the Griesbachian and Dienerian, the Smithian and Spathian substages, respectively. Thus, a total of six time bins (Changhsingian, Griesbachian, Dienerian, Smithian, Spathian, and Anisian) are employed to calculate biodiversity (taxonomic richness) and proportional extinction and origination rates. Species, genus, and family richness of each time bin were taken into account in examining biodiversity variations from the Changhsingian to Anisian. All genera have formal taxonomic names. And species of uncertain taxonomic status (i.e., Genus sp.) were included, in agreement with some of previous studies (Chen et al., 2011; Huang et al., 2014), but they were counted only once within each named genus in order to minimize taxonomic bias. The species qualified with terms like "cf." or "aff." are also included in this study. However, sample intensities are clearly variable across different geological periods, thus, rarefaction analysis (Raup, 1975) computed by the palaeontological software package PAST (Hammer et al., 2001) was implemented to test taxonomic bias (e.g., Chen et al., 2010, Chen et al., 2011). It is common to plot specimen counts against the numbers of a defined taxonomic rank (i.e. numbers of species or genera) in rarefaction analysis. Nevertheless, information on specimen counts is not available in the Paleobiology Database. Therefore, the rarefaction of occurrences against genera (Fig. 1A) and two adjacent taxonomic ranks plotted against each other (Fig. 1B) were both used herein. Concerning the latter, it is noteworthy that rarefaction analysis between two adjacent ranks (i.e. species/genus or genus/family) is likely to decrease or obscure the difference between diversity curves with relatively high confidence limits (i.e. 95% confidence limit) (Shen et al., 2000). Therefore, the rarefaction analysis of species richness against family richness is employed to determine sampling quality (Fig. 1B). Moreover, a confidence limit (95%) was used to examine the robustness of rarefaction curves. To better understand the taxonomic selectivity of bivalves through the P–Tr transition, all orders of this clade were investigated using biodiversity at different taxonomic levels.

To unravel the true extinction and recovery patterns of the Bivalvia over the P–Tr transition, we also calculated the proportional extinction and origination rates (Harper and Gallagher, 2001; Bambach et al., 2004) in each time bin, from the Changhsingian to Anisian at the species, genus, and family levels, respectively, according to the equations below:

Proportional Extinction rate = $N_{extin}/N_0 \times 100\%$,

Proportional Origination rate = $N_{orig}/N_0 \times 100\%$,

where N_0 represents the number of all taxa during certain stage (substage), N_{extin}/N_{orig} represents the number of extinction/origination taxa over the same interval, respectively. The 95% confidence interval of sample sizes was shown using the "Wilson Score Interval" method programmed in R software. Moreover, a Z-test was performed to examine the significance of the differences in extinction/origination rate between the next two time bins, which may provide some insights into the actual evolutionary patterns of the Bivalvia.

To shed light on the ecologic selectivity over the P–Tr transition, both taxonomic richness and proportional extinction/origination rates were employed to analyze the different physiological groups of bivalves at species, genus, and family levels, respectively. However, several physiological groups have a very small number of taxa in some time bins, which can bias understanding of true ecologic selectivity. Thus, we subdivided, collectively, the bivalves into two ecologic types: infaunal and epifaunal lifestyles. The former includes infaunal motile, infaunal slow-moving, and semi-infaunal motile, while the latter comprises epifaunal stationary and low-level epifaunal stationary. Their proportional extinction/origination rates were re-calculated. A Z-test was applied not only to test the significance of differences in richness between two adjacent time bins but also to examine the significance of proportional extinction/origination rates differences between the two ecologic groups (i.e. infauna and epifauna).

3. Results

3.1 The timing and patterns of extinction-recovery of bivalves

3.1.1 Biodiversity changes

Compared with some typical Paleozoic-type clades (i.e. brachiopods, crinoids, and rugose corals), bivalves underwent a less marked biodiversity turnover over the P–Tr boundary. Pre-extinction Changhsingian bivalves are very diverse, including 368 species, 118 genera, and 47 families. Their biodiversity declined by ~56%, 62%, and 43% at the species, genus, and family levels, respectively in the PTME, and only 162 species, 45 genera and 27 families occur in the Griesbachian (Fig. 2).

Another apparent decline in biodiversity occurred throughout part or all of the Griesbachian, with drops of ~69%, 42%, and 22% species, genera, and families, respectively. Surprisingly, the Dienerian witnessed the lowest taxonomic richness within all Early Triassic time bins, having only 50 species, 26 genera, and 21 families (Fig. 2).

The Smithian saw the first increase in richness at all taxonomic levels after the PTME, with a surge of 128%, 69%, and 43%, to levels of 144 species, 44 genera, and 30 families in this time bin (Fig. 2). Biodiversity further increased through time, with 172 species, 73 genera and 36 families present in the Spathian (Fig. 2).

Biodiversity continued to rise to a peak in the Anisian, up to, surprisingly, 424 species, 123 genera, and 57 families (Fig. 2), with increases of 146%, 68%, and 58%, respectively from the last time bin. Such a pronounced increase in biodiversity signals a major radiation of this clade following the P–Tr biotic crisis (Komatsu et al., 2004).

The P–Tr biodiversity change apparently exhibits a persistent decline from the latest Permian (i.e. Changhsingian) up to the Dienerian, with the first proliferation in the Smithian and a stepwise recovery through the Smithian to Anisian when this clade dramatically diversified. However, both sampling bias and the Lazarus effect in terms of biodiversity may, to some extent, obscure the true pattern. Therefore, when the initial recovery of this group occurred remains unknown.

3.1.2 Taxonomic selectivity

The Changhsingian assemblage is very diverse and includes 16 orders (Fig. 3; Table S1). The Pectinida is the most diverse group, containing 162 species accounting for 44% of total taxa, followed by the Ostreida, Myalinida, Trigoniida, and Cardiida (Fig. 3; Table S1). The remaining orders include only a small number of species.

Intriguingly, all the orders survived the PTME although they behaved distinctively during the crisis and its aftermath. The Pholadida, Solemyida, Modiomorphida, and Arcida vanished in the Griesbachian, but re-appeared in the late Early Triassic, probably indicating a Lazarus effect (Jablonski, 1996; Wignall and Benton, 1999; Twitchett, 2000; Fara, 2001; Rickards and Wright, 2002). The Pholadomyida (with a decline of 92% species), Carditida (92%), Nuculanida (86%), and Pterioida (86%) all suffered dramatic biodiversity drops in the PTME. In contrast, the Ostreida experienced only a moderate to minor reduction in biodiversity across the P–Tr boundary, with a decrease of ~31% species. The Griesbachian bivalves show almost no difference from the Changhsingian assemblage in terms of the compositions of the major groups. The Pectinida is the predominant group, accounting for 56% of total species, followed by the Ostreida, Myalinida, and Trigoniida (Fig. 3; Table S1).

The Dienerian witnessed an apparent depletion in biodiversity relative to the Griesbachian. Of these, six groups (i.e., the Arcida, Lucinina, Modiomorphida, Pterioida, Mytilida, Nuculida, and Solemyida) disappeared in this interval, but re-appeared in the late Early Triassic, signaling a Lazarus effect. Like the Griesbachian assemblage, the Dienerian faunas are also dominated by the Pectinida representing ~38% of total species. However, the importance of three groups, the Myalinida, Ostreida, and Trigoniida (Fig. 3; Table S1) is almost equivalent, at least in terms of richness.

Biodiversity proliferated during the Smithian. The fauna was dominated by the Pectinida, followed by the Ostreida, Trigoniida and Myalinida (Fig. 3; Table S1). Apart from those major groups, diversification of other groups also characterized this substage, like the Nuculanida, Ostreida, and Pectinida. The Spathian bivalves experienced a minor increase in biodiversity and are dominated by the Pectinida,

followed by the Ostreida and Trigoniida, exhibiting a similar taxonomic composition to the Smithian assemblage. However, the Nuculanida, instead of the Myalinida, became the fourth most diverse group (Fig. 3; Table S1).

All orders increased in richness in the Anisian, coupled with the appearance of some new groups (i.e. the Hiatellida, Megalodontida, and Pandorida). The Ostreida replaced the Pectinida and was now the most diverse group at the species level. While the Pectinida remained the predominant group at the genus, and family levels. The Trigoniida, Mytilida, Cardiida, Carditida, and Nuculanida (Fig. 3; Table S1) are all major players that contributed to the Anisian radiation of the entire clade.

To sum up, the Ostreida, Trigoniida, and Mytilida performed well during the PTME and responded well to any subsequent environmental stresses; the richness of these groups rebounded in the Anisian. In contrast, the Pectinida, Myalinida, and Pholadomyida suffered from the end-Permian 'Great Dying'. Bivalves also underwent a switch of dominance in communities from the Pectinida to the Ostreida between the Spathian and Anisian, although the presence of this turnover remains to be further examined due to the availability of only one single interval for sampling.

3.1.3 Proportional extinction/origination rates

Proportional origination rates are very low among the Changhsingian bivalves, exhibiting 54%, 19%, and 4%, at the species, genus, and family levels, respectively. Their proportional extinction rates at the end of the Changhsingian are moderate to high, up to 85%, 64%, 32% at the species, genus, and family levels, respectively (Fig. 4; Table 1); slightly higher than previous estimates for all taxonomic levels.

Intriguingly, the specific origination rate is high in the Griesbachian, approaching 75%, which is significantly different from the same proxy in the Changhsingian ($p<0.05$). Conversely, the proportion extinction rates at all taxonomic levels display low to moderate levels (Fig. 4; Table 1), also clearly differing from the same proxies in the previous interval ($p<0.05$). Accordingly, the relatively high proportional origination rates, low proportional extinction rates, coupled with a high biodiversity, indicate that the initial recovery of bivalves may have occurred in the

Griesbachian.

In the Dienerian, bivalves suffered a moderate proportional extinction rate at the species level (68%) and much lower extinction rates at the genus (19%) and family (19%) levels. The proportional origination rates show similar patterns (52%, 19%, 10%). It is noteworthy that the specific origination rate is significantly lower than that of the Griesbachian faunas ($p<0.05$) (Fig. 4; Table 1). Moreover, similar proportional extinction/origination rate patterns are also seen in the Smithian (Fig. 4; Table 1). The proportional origination rates in the Spathian (62%, 33%, 8%) show no difference from the same proxies in the Smithian ($p>0.05$). However, their proportional extinction rates (79%, 30%, 17%) are higher than their counterparts in the Smithian (Fig. 4; Table 1). In particular, the specific extinction rate differs clearly from that in the Smithian ($p<0.05$). Such high extinction rates suggest that many species were already extinct prior to the Anisian.

The Anisian saw a striking increase in proportional origination rates (83%, 52%, 37%) (Fig. 4; Table 1), showing significant difference at all levels from the Spathian proxies ($p<0.05$). The Anisian bivalves are thus very different from the Spathian faunas in composition. Such a high specific origination rate indicates that speciation progressed vigorously in the Anisian, and thus contributed significantly to the radiation within this interval. Surprisingly, proportional extinction rates (75%, 37%, 20%) are also elevated (Fig. 4; Table 1), indicating the rapid evolutionary rates of the bivalves at this time.

3.2 Ecologic selectivity

3.2.1 Biodiversity changes among lifestyles of bivalves

Within the Changhsingian bivalve assemblages, the stationary epifauna is the most diverse, accounting for 54% of all species, followed by the motile infauna and the stationary low-level epifauna. The other two life modes of bivalves (i.e. the slow-moving infauna and motile semi-infauna) (Fig. 5; Table S2) account for relatively low percentages. All life modes survived the PTME, although the motile

semi-infauna disappeared during the biotic crisis but re-appeared afterwards. The stationary low-level epifauna and motile infauna declined by~76% and 67% at species levels, respectively, ranking them as the main victims of the PTME. In contrast, the stationary epifauna experienced a lesser depletion, ~42%.

Following the PTME, the stationary epifauna dominated the Griesbachian, followed by the motile infauna, slow-moving infauna and the stationary low-level epifauna (Fig. 5; Table S2). Both the slow-moving infauna and stationary epifauna experienced a remarkable reduction in biodiversity through part or all of the Griesbachian, with only a very few species persisting into the Dienerian (Fig. 5; Table S2).

Bivalves, irrespective of their lifestyles, all underwent the first post-extinction proliferation in the Smithian. The stationary epifauna was particularly diverse, increasing 185% at the species level from the Dienerian assemblage. And the motile infauna also diversified in the same time bin (Fig. 5; Table S2). Such lifestyles extended to the Spathian. Subsequently, all bivalve life modes radiated in the Anisian when the motile semi-infauna experienced an amazing increase, ~350%, 300%, and 300% at the species, genus, and family levels, respectively, followed by the stationary low-level epifauna (357%, 120%, 50%) and motile infauna (159%, 85%, 73%).

Accordingly, the dominance of various lifestyles in each time bin remained almost unchanged from the Changhsingian to Anisian; any changes in the ecological preferences of the bivalves were not obvious before and after the PTME.

3.2.2 Proportions of extinction/origination rates among lifestyles

On the basis of proportional extinction/origination rates, the extinction-recovery patterns vary amongst different life modes through the P–Tr transition (Fig. 6; Table S2). However, there is worthy of note that the motile infauna and stationary epifauna dominated the bivalve assemblages in all time bins and other life modes (e.g., the stationary low-level epifauna, slow-moving infauna, and motile semi-infauna) usually consist of a very small number of species. Such small numbers of taxa may bias the selectivity patterns if each life mode is calculated separately. Accordingly, all bivalves

have been re-categorized into two simple lifestyles: the infauna and epifauna.

3.2.2.1 Infauna

The Changhsingian infaunal bivalves suffered very high extinction rates, up to 87%, 65%, and 32% at the species, genus, and family levels, respectively during the PTME (Fig. 7; Table 2). In the Griesbachian, this lifestyle group displayed rather high proportional origination rates at the species level, up to 70% and relatively low extinction rates (Fig. 7; Table 2). Surprisingly, 74% of species in the Dienerian infauna are newcomers.

Infaunal bivalves exhibit similar proportional extinction/origination rates between the Smithian and Spathian. Their proportional origination rates increased markedly in the Anisian, surging from 59%, 33%, and 6% in the Spathian to 82%, 54%, and 39% at the species, genus, and family levels, respectively (Fig. 7; Table 2). Both specific and familial origination rates are significantly different ($p<0.05$) from the same proxies in the Spathian. The elevated origination rates, coupled with high extinction rates in Spathian, suggest rapid speciation and turnover during the Anisian.

3.2.2.2 Epifauna

Like the infaunal elements, the Changhsingian epifaunal bivalves also suffered high proportional extinction rates, up to 85%, 61%, and 21% at the species, genus, and family levels, respectively during the P–T 'Great Dying'. In the Griesbachian, the epifauna experienced much higher ($p<0.05$) origination rates at the species level, and lower extinction rates, particularly in the species and genus levels ($p<0.05$) than those in the Changhsingian (Fig. 7; Table 2). As a consequence, the composition of epifaunal assemblages changed significantly across the P–Tr boundary.

The epifaunal group experienced relatively low proportional extinction rates (48%, 8%, 0%) and origination rates (33%, 8%, 0%) in the Dienerian (Fig. 7; Table 2). Importantly the specific origination rate differs significantly ($p<0.05$), from that in the Griesbachian. While, in the Smithian, the epifaunal taxa possessed high proportional origination rates at the species level, differing significantly ($p<0.05$) from the

counterparts in the Dienerian. In contrast, their extinction rates (65%, 15%, 6%) exhibit a minor increase (Fig. 7; Table 2) with no significant difference ($p>0.05$) from Dienerian proxies. The proportional extinction/origination rates of the epifaunal taxa overall show no significant change from the Smithian to Spathian.

In the Anisian, epifaunal bivalves exhibit similar patterns in terms of proportional extinction/origination rate to those of the infaunal group, marked by high origination rates (85%, 50%, 30%), differing significantly ($p<0.05$) from those of the Spathian at the species level, and high extinction rates (73%, 31%, 15%) (Fig. 7; Table 2), showing no significant difference ($p>0.05$) from the counterparts in the Spathian. The high origination rates, coupled with high extinction rates in Spathian, indicate species turnover within the epifauna during the Anisian.

3.2.2.3 Comparison between the infauna and epifauna

A Z-test was employed to examine the significance of differences with respect to proportional extinction/origination rates between the infauna and epifauna through the P–Tr transition. At the species level, the Griesbachian witnessed a significant ($p<0.05$) higher extinction rate within the epifauna when compared with that within the infaunal group. The epifauna had significant ($p<0.05$) higher origination rates in the Changhsingian and Smithian, but much ($p<0.05$) lower origination rates in the Dienerian, than the other group. No significant difference ($p>0.05$) is observed at the genus and family levels within any time bin from the Changhsingian to Anisian.

4. Discussion

4.1 The extinction-recovery patterns of the P–Tr bivalves

The fossil record from South China suggests that bivalves experienced a single-phase mass extinction across the P–Tr boundary (Huang et al., 2014). The PTME therefore is considered as a mono-episode biotic crisis in this study. When compared to other clades (i.e. brachiopods, corals, and echinoids) (Wang and

390 Sugiyama, 2000; Twitchett and Oji, 2005; Chen et al., 2005a, b; Chen and McNamara,
391 2006), bivalves suffered a lesser, typically moderate extinction, indicated by the
392 proportional extinction rate at the genus level during the P–Tr 'Great Dying'
393 (Nakazawa and Runnegar, 1973; Yin, 1985, 1987; Li, 1995; Fang, 2004; Huang et al.,
394 2014). The newly updated global dataset also strengthens this view as bivalves
395 suffered an extinction rate of 64% at the genus level associated with 85% and 32% at
396 the species and family levels, respectively. The structure of the marine ecosystem,
397 however, had undergone the greatest turnover over the P–Tr boundary, featured by the
398 switch of the predominant composition from the Paleozoic EF to the Modern EF,
399 coincident with changes in the lifestyles and physiology of both the survivors and
400 newcomers (Raup, 1979; Sepkoski, 1981; Bambach et al., 2002; Wagner et al., 2006;
401 Leighton et al., 2013).
402 The general picture of global biodiversity shows that bivalves underwent a
403 stepwise depletion in biodiversity through the Changhsingian–Dienerian interval. The
404 lowest biodiversity occurred in the Dienerian, implying that extinction might
405 continuously occur through part or all of the Griesbachian, except for the PTME (Fig.
406 2). However, taxonomic bias may obscure the real evolutionary patterns of bivalves.
407 Thus, more rigorous analyses are required combined with the other important proxies,
408 such as the proportional extinction/origination rates (Harper and Gallagher, 2001;
409 Bambach et al., 2004).
410 As stated above, bivalves experienced very high origination rates and relatively
411 low extinction rates in the Griesbachian (Fig. 4; Table 1), when the Paleozoic-type (i.e.
412 bivalve species appeared prior to the P–Tr biocrisis) accounted for only ~25% (Table
413 S3). Previously, marine benthic communities were believed to be dominated by
414 survivors from the Permian and several progenitors such as *Claraia* and the
415 *Eumorphotis* in the Early Triassic (Hallam and Wignall, 1997; Komatsu et al., 2008),
416 and did not diversify until early Middle Triassic (Chen, 2004; Komatsu et al., 2004,
417 2010). In fact progenitor taxa (i.e., species of *Claraia* and *Eumorphotis*) occupy 42%
418 of all species and 46% of all newcomers in the Griesbachian, even with the possible
419 over-splitting of *Claraia* (Table S4). Thus, the majority of the Griesbachian taxa are

420 non-progenitors.

421 Bivalves suffered a rather high origination rate, coincident with relatively low
422 proportional extinction rates in the Griesbachian (Fig. 4; Table 1). The high
423 biodiversity therefore is possibly driven by the presence of many newcomers
424 associated with rapid speciation. The combination of a relatively high biodiversity,
425 high origination rate, and low extinction rate indicates that an initial recovery of
426 bivalves occurred in the Griesbachian, reinforced by the presence of the diverse
427 bivalve communities of the lowest Triassic carbonates of Guangxi, South China
428 (Hautmann et al., 2011) and the Lower Triassic Werfen Formation, northern Italy
429 (Hofmann et al., 2015).

430 The rather low extinction rate in the Griesbachian (Fig. 4; Table 1) rejects the
431 possibility of a biotic extinction between the Griesbachian and Dienerian. The lowest
432 biodiversity in the Dienerian (Fig. 2) is probably biased by a Lazarus effect (Jablonski,
433 1996), a phenomenon commonly present in major mass extinction episodes and that
434 also occurs in other time intervals (attributed to the incompleteness of fossil record)
435 (Wignall and Benton, 1999; Twitchett, 2000; Fara, 2001; Rickards and Wright, 2002).
436 Thus, the bivalve assemblage in each time bin is taxonomically categorized into
437 newcomers, survivors from the preceding time bin, and survivors persisting from
438 earlier time bins (Table S5). The numbers of Lazarus taxa in each sampling time bin
439 from the Griesbachian to Spathian (Table S6) were also counted. Both proxies
440 indicate that the Dienerian and Smithian richness have been significantly biased by
441 the Lazarus effect. Griesbachian bivalves had a low extinction rate, many disappeared
442 in Dienerian, but re-appeared afterwards. The Dienerian biodiversity therefore
443 remained low.

444 Similarly, a high origination rate, concurrent with an elevated biodiversity in
445 the Smithian (Figs 2, 4; Table 1), indicates the proliferation of this group in the
446 Smithian. And the rather low extinction rate in the Smithian (Fig. 4; Table 1) implies
447 that the faunal composition of assemblages remained nearly unchanged between the
448 Smithian and Spathian. Moreover, another evolutionary revolution of bivalves
449 occurred probably in the Anisian, Middle Triassic. Although bivalves exhibited a high

extinction rate in the Spathian, they reached their highest biodiversity, incorporating markedly elevated origination rate in the Anisian (Fig. 2, 4; Table 1). Consequently, the dramatic increase in biodiversity was contributed by the appearance of new taxa (Table 1), which also suggests a rapid speciation at that time. In addition, faunal compositions greatly changed from the Smithian to Anisian. The Paleozoic EF occupied 13% of all species and 45% of all genera in the Smithian assemblages, while the percentage declined to 5% and 29% at the species and genus levels, respectively in the Anisian bivalves (Table S3). All the lines of evidence indicate the bivalve radiation took place in the Anisian, as suggested in earlier studies (Komatsu et al., 2004, 2010; Ros and Echevarría, 2011; Ros et al., 2011; Chen and Benton, 2012).

4.2 Ecologic selectivity between the infauna and epifauna

The data from South China display a lack of ecologic selectivity among bivalves through the P–Tr biotic crisis (Huang et al., 2014). The proportional extinction rates calculated from the new global dataset show no significant differences ($p>0.05$) between the infaunal and epifaunal lifestyles by the end of the Permian (Fig. 7; Table 2).

Infaunalization, particularly involving bivalves, was thought to be prevalent in Mesozoic oceans (Vermeij, 1977; Thayer, 1979). The epifaunal taxa exhibit higher extinction rates than those of the infauna, while the origination rates between the two groups show no significant difference at the genus level through the entire Triassic (McRoberts, 2001). Our study suggests, however, that the epifauna exhibits a significantly higher biodiversity than the infauna in any given time bins after the PTME (Fig. 5; Table S2). The proportions of the representative infaunal (i.e. the Cardiida) and epifaunal taxa (i.e. the Pectinida) exhibit neither increasing nor decreasing trends throughout the P–Tr transition (Table S7A). In addition, the proportion of all infaunal taxa within all the benthic communities is also calculated, which remains almost unchanged before and after the PTME (i.e. the Changhsingian and Anisian) (Table S7B), although infaunal bivalves may proliferate locally in

particular habitats in the Anisian (i.e. storm- and wave-dominated shelf, Komatsu et al., 2010). Latest study also suggests that the roles are minor played by mass extinctions, including PTME into ecospace utilization of the bivalves, despite their impacts on biodiversity (Mondal and Harries, 2016). Our observation is in agreement with the previous view that the elevated infaunalization among bivalves did not occur before the latest Triassic (Ros and Echevarría, 2011; Ros et al., 2011). More importantly, no significant difference ($p>0.05$) is shown in proportional extinction/origination rates at the genus level between the infaunal and epifaunal groups in any time bins, at least prior to the Ladinian. Nevertheless, the proportional extinction/origination rates are occasionally different between the two lifestyle bivalves at the species level. For instance, the epifauna had a higher specific extinction rate than the infauna in the Griesbachian (Fig. 7; Table 2). This is probably due to the disappearance of both *Claraia* and *Eumorphotis* (25 out of 68 species disappeared). Anyway, in view of generic proportional extinction/origination rates, no significant ecological preference can be observed in any given time bins prior to the Ladinian (Fig. 7).

4.3. Driving force of the Mesozoic Marine Revolution

The Mesozoic Marine Revolution (MMR) is considered to be one of the key Phanerozoic radiations, marked by the final establishment of the Modern EF in marine ecosystems. The MMR is generally thought to be driven by escalating interactions between organisms, especially the substantial increase in the intensity of predation (Vermeij, 1977; Roy, 1994; McRoberts, 2001; Kerr and Kelley, 2015). Such biotic interactions could drive adaptations, including efficient escape and defence strategies. However, crucial is the ability to take advantage of new ecospace such as infaunal habitats, free from surface-dwelling predators (Vermeij, 1977; Signor and Brett, 1984; Harper and Skelton, 1993; Roy, 1994; McRoberts, 2001). Growing evidence shows that the MMR may have originated in Early-Middle Triassic (McRoberts, 2001; Baumiller et al., 2010; Gorzelak et al., 2012; Brachaniec et al.,

510 2015). If escalating predation pressure indeed played a critical role in initially driving
511 the MMR, infaunalization then would not be prevalent before the Ladinian,
512 inconsistent with the earlier estimates (McRoberts, 2001). Though a
513 three-dimensional, relatively vacant (Sheehan, 1996) and stable ecospace provided an
514 unrivalled opportunity for the infaunal bivalves to diversify, high origination rates
515 within the epifauna might be expected while they faced environmental stresses such
516 as fluctuating seawater temperature, salinity, and energy flow as well as potential
517 competition among organisms. There is, however, no significant difference in
518 proportional extinction/origination rates between the epifauna and infauna, at least,
519 before the Ladinian. Thus, the MMR marked by the elevated infaunalization of
520 bivalves may not be evident until latest Triassic (Ros and Echevarría, 2011; Ros et al.,
521 2011). Alternatively, the infaunalization may not have been involved in the initial
522 evolution of the MMR. Hautmann et al. (2015) also suggested that the interspecific
523 interactions were very weak in the intermediate aftermath of the greatest biotic crisis,
524 occurring at a timescale much longer than at background timescales. As a result,
525 physical factors such as amelioration of marine environments in the late Early Triassic
526 (Hofmann et al., 2013, 2015; Zhang et al., 2015) may have driven the origination and
527 early evolution of the MMR, which is reinforced by a very rare fossil record of
528 predatory activities through the Early Triassic (McRoberts, 2001). Both intrinsic and
529 extrinsic drivers have contributed to long-term macroevolution. Critical is an
530 understanding the applicability and consequences of 'Red Queen' model (i.e.
531 large-scale evolution is driven by interactions between organisms) in contrast to the
532 so-called 'Court Jester' model (i.e. the critical driver is the physical environment)
533 (Benton, 2009; Chen and Benton, 2012). The latter appears more relevant during the
534 widely fluctuating environmental conditions during the earlier parts of the Triassic,
535 setting a template for a later applicability of Red Queen interactions.
536
537 **5. Conclusion**
538
539 The updated global dataset shows that bivalves experienced less, typically

moderate extinction during the P–Tr biotic crisis. Both biodiversity and proportional extinction/origination rates indicate an initial recovery of the bivalves in the Griesbachian. Thus, no survival stage is recognized in the immediate post-extinction bivalves. The extremely low biodiversity in the Dienerian is possibly biased by a strong Lazarus effect. Bivalves underwent a stepwise recovery from the Dienerian to Anisian with the proliferation in the Smithian. The Anisian witnessed the major radiation of bivalves after the PTME, which is marked by t an elevated richness and rather high origination rates. Taxonomically, the Ostreida, Trigoniida, and Mytilida may have benefited from the PTME and the associated devastation of many environments, while the other three orders, the Pectinida, Myalinida, and Pholadomyida suffered from this biotic crisis, in terms of biodiversity variations before and after PTME. No ecologic selectivity is present between the infaunal and epifaunal bivalves at the genus level in the aftermath of the PTME, evidenced by a lack of significant difference of proportional extinction/origination rates in any given time bins prior to the Ladinian. Infaunalization is one of the most efficient strategies to escape from the predatory pressure. If the MMR is indeed driven by organismal interactions, the infaunalization did not occur, at least prior to the Ladinian (Middle Triassic). Alternatively, the start of the MMR was probably not driven by biotic processes associated with escalating predation pressure (‘Red Queen’ model).Instead, environmental changes, like the amelioration of extreme physical and chemical environments (‘Court Jester’ model) in the late Early Triassic may be responsible for the origination and initial evolution of the MMR.

Acknowledgements

The first author thanks Margaret L. Fraiser for hosting his short visiting in the summer of 2014 and sharing many ideas on the P–Tr evolution of bivalves. We are grateful to Matthew Clapham for the critical comments and constructive suggestions, which have greatly improved the quality of this paper. We also thank the major contributors to the Paleobiology Database: Matthew Clapham, Wolfgang Kiessling, Richard Butler, David Bottjer, and Alistair McGowan for their contributions to the

dataset. We are also grateful to Hongfu Yin for his help in critically reviewing dataset of the global P–Tr bivalves used in this study. This study was supported by the 111Program of China, Ministry of Education of China, a NSFC grant (No41272023), and two research grants from the State Key Laboratory of Biogeology and Environmental Geology, China University of Geosciences (GBL11206) and the State Key Laboratory of Geological Processes and Mineral Resources, China University of Geosciences (GPMR201302). Harper thanks the Leverhulme Trust for support. It is a contribution to IGCP 630.

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Figure and table captions

Fig. 1. Rarefaction curves with 95% confidence limits for bivalves from the Changhsingian to Anisian. (A) The genus richness versus the number of occurrences. (B) family richness versus species richness.

Fig. 2. Taxonomic richness of bivalve species, genera and families through the P–Tr transition. Gr. = Griesbachian, Di. = Dienerian, Sm. = Smithian. The scale is shown.

Fig. 3. Numbers of species, genera and families of the major bivalve orders from the Changhsingian to Anisian showing taxonomic selectivity during extinction-recovery intervals. Arc. = Arcida, Modio. = Modiomorphida, Nucula. = Nuculanida, Nucu. = Nuculida, Phola. = Pholadida, Trigon. = Trigoniida, Pholado. = Pholadomyida, Myti. = Mytilida, Pteri. = Pterioida, Sole. = Solemyida, M.+P.+H. = Megalodontida + Pandorida + Hiatellida. The scale is shown.

Fig. 4. Proportional extinction (blue bar) and origination (pink bar) rates of bivalve species, genera and families from the Changhsingian to Anisian. Scale bars represent

95% confidence interval of sample sizes using the “Wilson score interval” method calculated with R software.

Fig. 5. Taxonomic richness at the species, genus, and family levels among different bivalve life modes from the Changhsingian to Anisian. Mo.se.-inf. = Mobile semi-infauna, Sl.-m.inf. = slow-moving infauna, Sta.low-level epi. = stationary low-level epifauna; Gr. = Griesbachian, Di. = Dienerian, Sm. = Smithian. The scale is shown.

Fig. 6. Proportional extinction and origination rates among various bivalve life modes at the species, genus, and family levels, respectively, from the Changhsingian to Anisian.

Fig. 7. Proportional extinction and origination rates between the infaunal and epifaunal bivalves at the species, genus, and family levels, respectively, from the Changhsingian to Anisian. Scale bars represent 95% confidence interval of sample sizes using the “Wilson score interval” method.

Table 1. Quantitative data on proportional extinction and origination rates of bivalve species, genera and families from the Changhsingian to Anisian. Changhs. = Changhsingian, Griesba. = Griesbachian, Diene. = Dienerian.

Table 2. Quantitative data on proportional extinction and origination rates between the infaunal and epifaunal bivalves at the species, genus and family levels, respectively, from the Changhsingian to Anisian. Changhs. = Changhsingian, Griesba. = Griesbachian, Dien. = Dienerian.

Online Supplementary Material:

Table S1. Quantitative data on species, genus, and family taxonomic richness among

840 all orders of bivalves from the Changhsingian to Anisian.

841

842 Table S2. Quantitative data on taxonomic richness and proportional extinction/
843 origination rates among various bivalve life modes at the species, genus, and family
844 levels from the Changhsingian to Anisian. Mobile semi-inf. = mobile semi-infauna,
845 slow-m.infa. = slow-moving infauna, sta.low-level epi. = stationary low-level
846 epifauna.

847

848 Table S3. Quantitative data showing species and genus counts of the number and
849 percentage of the Paleozoic-type bivalves in the aftermath of the PTME. Griesba. =
850 Griesbachian.

851

852 Table S4. Quantitative data showing counts of the number and percentage of *Claraia*
853 and *Eumorphotis* species out of the total taxa and origination taxa in the Griesbachian
854 and Dienerian intervals. Orig. = Origination.

855

856 Table S5. Quantitative data showing the newcomers, survivors from the preceding
857 interval, and survivors persisting from earlier intervals. Numbers and proportions are
858 shown herein. Griesba. = Griesbachian.

859

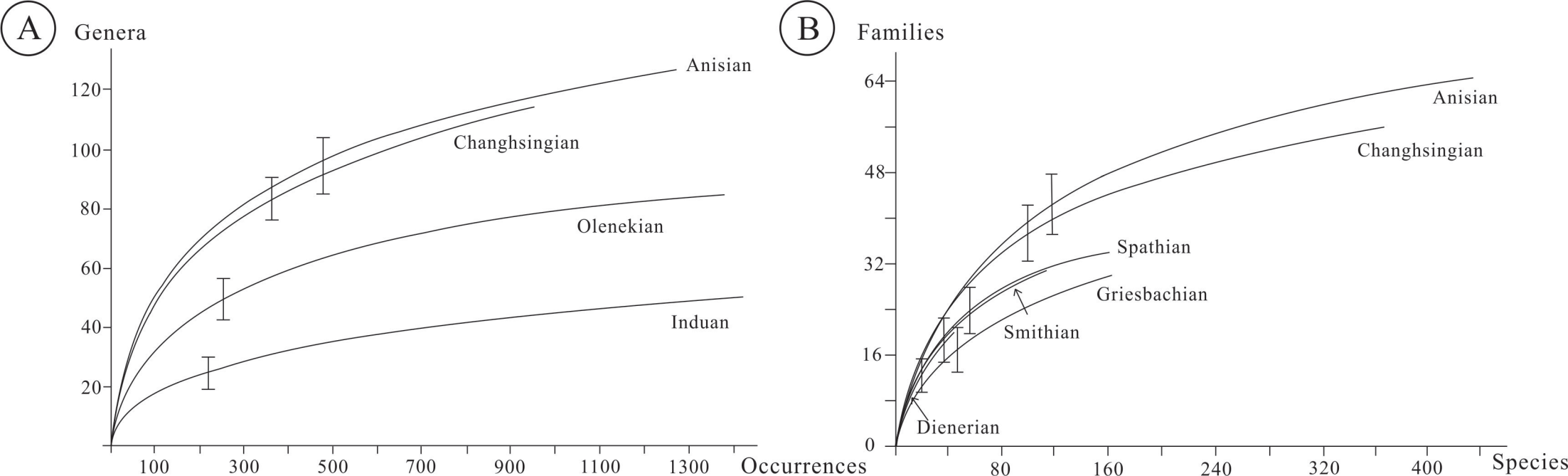
860 Table S6. Generic and specific data testing the Lazarus effect on biodiversity trends.
861 Lazarus taxa are defined as 'disappearance and apparent extinction of taxa that later
862 reappear unscathed' in fossil record. Note that the Dienerian and Smithian
863 biodiversities were greatly influenced by the Lazarus effect. Griesba. = Griesbachian,
864 Diene. = Dienerian, Smith. = Smithian, Spath. = Spathian.

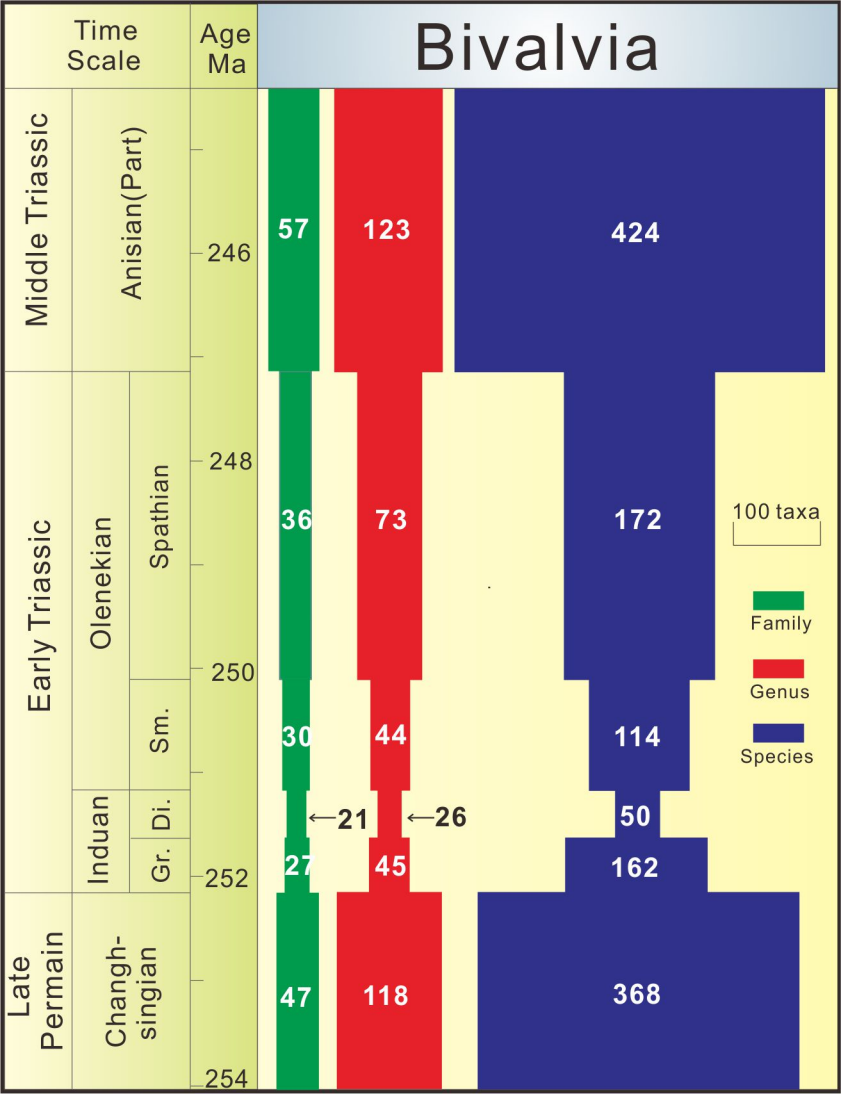
865

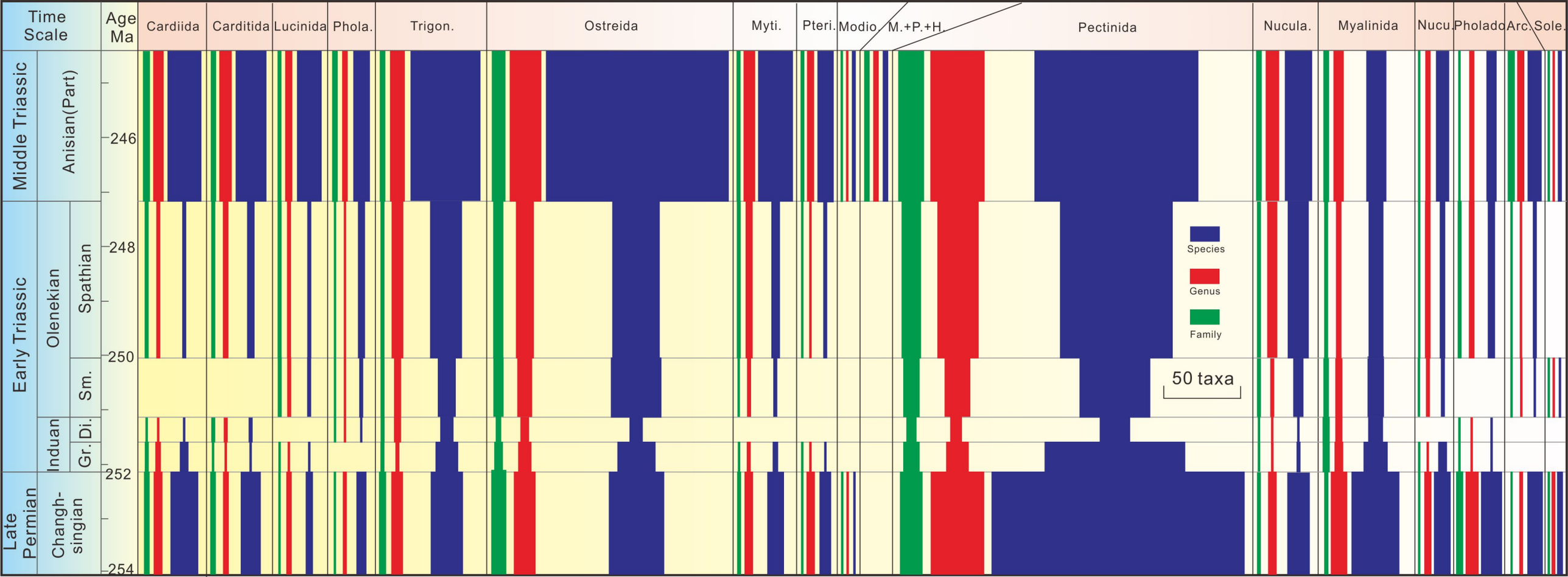
866 Table S7. (A) Quantitative data showing proportions of the representative infaunal
867 (i.e.the order of Cardiida) and epifaunal taxa (i.e. the order of Pectinida) before and
868 after the PTME. (B) Proportions of (all) the infaunal taxa (versus epifaunal taxa)
869 within the benthic communities throughout the interval. Changhs. = Changhsingian,

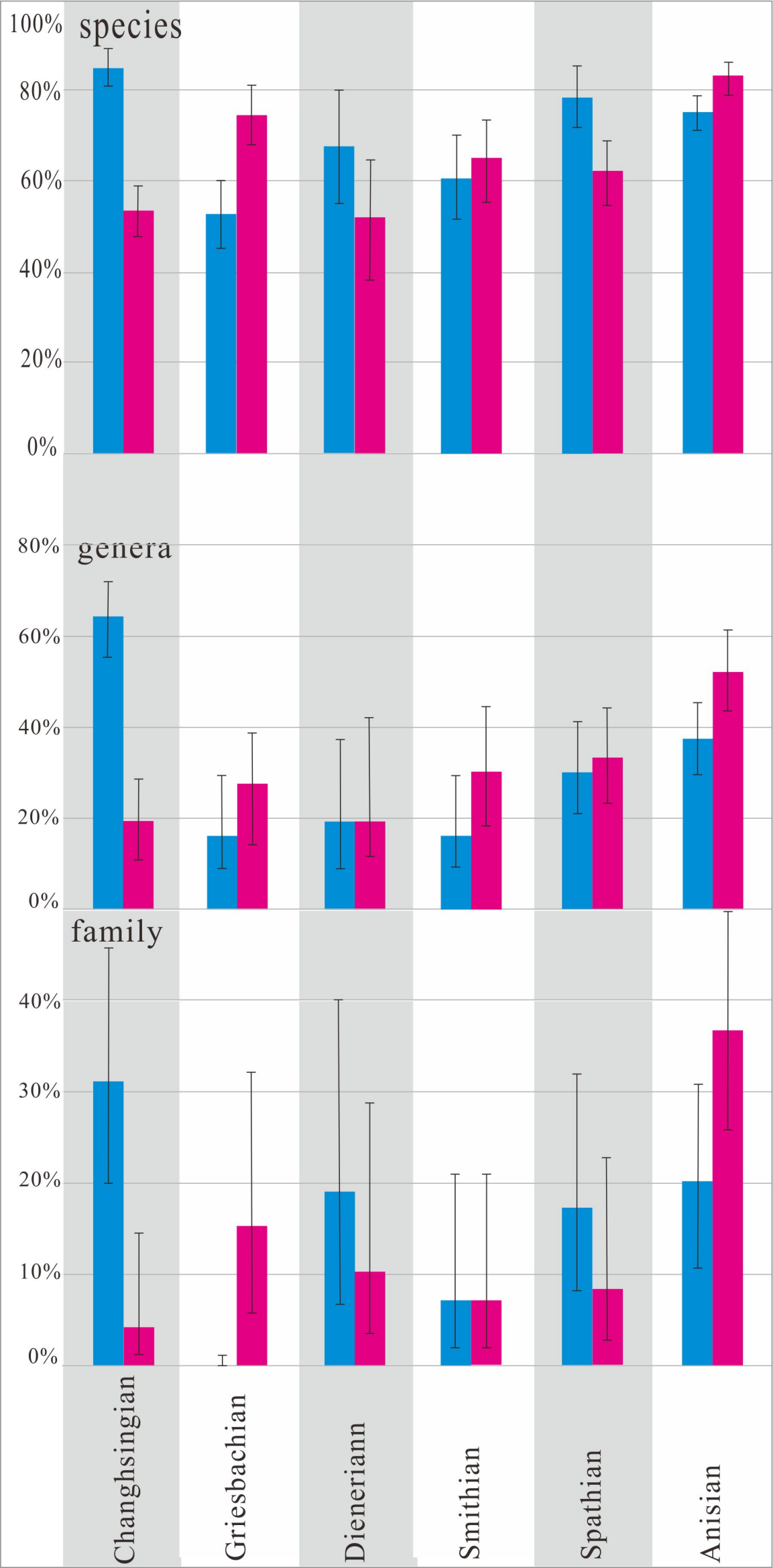
870 Griesba. = Griesbachian, Diene. = Dienerian, Smith. = Smithian, Spath. = Spathian.

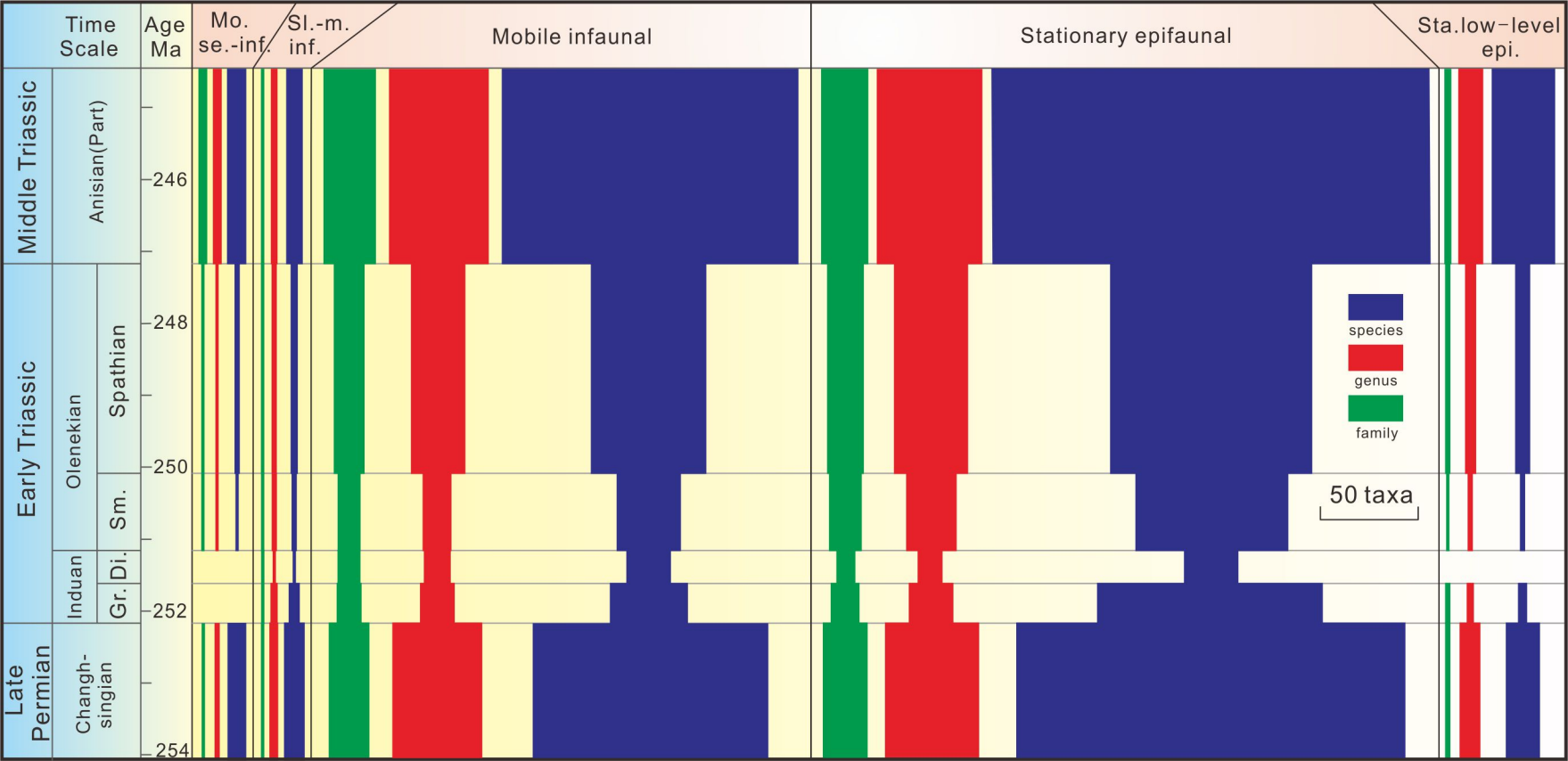
871 RI = Representative infaunal taxa, RE = Representative epifaunal taxa.


A
Genera
120
100
80
60
40
20
Anisian
Changhsingian
Olenekian
Induan
100
300
500
700
900
1100
1300
Occurrences
B
Families
64
48
32
16
0
Anisian
Changhsingian
Spathian
Griesbachian
Smithian
Dienerian
80
160
240
320
400
Species


Time Scale
Age Ma
Bivalvia
Middle Triassic
Anisian(Part)
Early Triassic
Olenekian
Spathian
Sm.
Induan
Di.
Gr.
Late Permain
Changh-singian
246
248
250
252
254
57
123
424
36
73
172
30
44
114
←21
←26
50
27
45
162
47
118
368
100 taxa
Family
Genus
Species


Time Scale
Age Ma
Cardiida
Carditida
Lucinida
Phola.
Trigon.
Ostreida
Myti.
Pteri.
Modio.
M.+P.+H.
Pectinida
Nucula.
Myalinida
Nucu.
Pholado
Arc.
Sole.
Middle Triassic
Anisian(Part)
Early Triassic
Olenekian
Spathian
Sm.
Induan
Di.
Gr.
Late Permian
Changh-singian
246
248
250
252
254
Species
Genus
Family
50 taxa


species
100%
80%
60%
40%
20%
0%
genera
80%
60%
40%
20%
0%
family
40%
30%
20%
10%
0%
Changhsingian
Griesbachian
Dienerian
Smithian
Spathian
Anisian


Time Scale
Age Ma
Mo. se.-inf.
Sl.-m. inf.
Mobile infaunal
Stationary epifaunal
Sta.low-level epi.
Middle Triassic
Anisian(Part)
Early Triassic
Olenekian
Spathian
Sm.
Induan
Di.
Gr.
Late Permian
Changh-singian
246
248
250
252
254
species
genus
family
50 taxa

extinction rates

100%
80%
60%
40%
20%
0%

Species

0

100

Genera

100

Family

80%
60%
40%
30%
20%
10%
0%

origination rates

100%
90%
80%
70%
60%
50%
40%
30%
80%
60%
40%
20%
0%
80%
60%
40%
20%
0%

Species

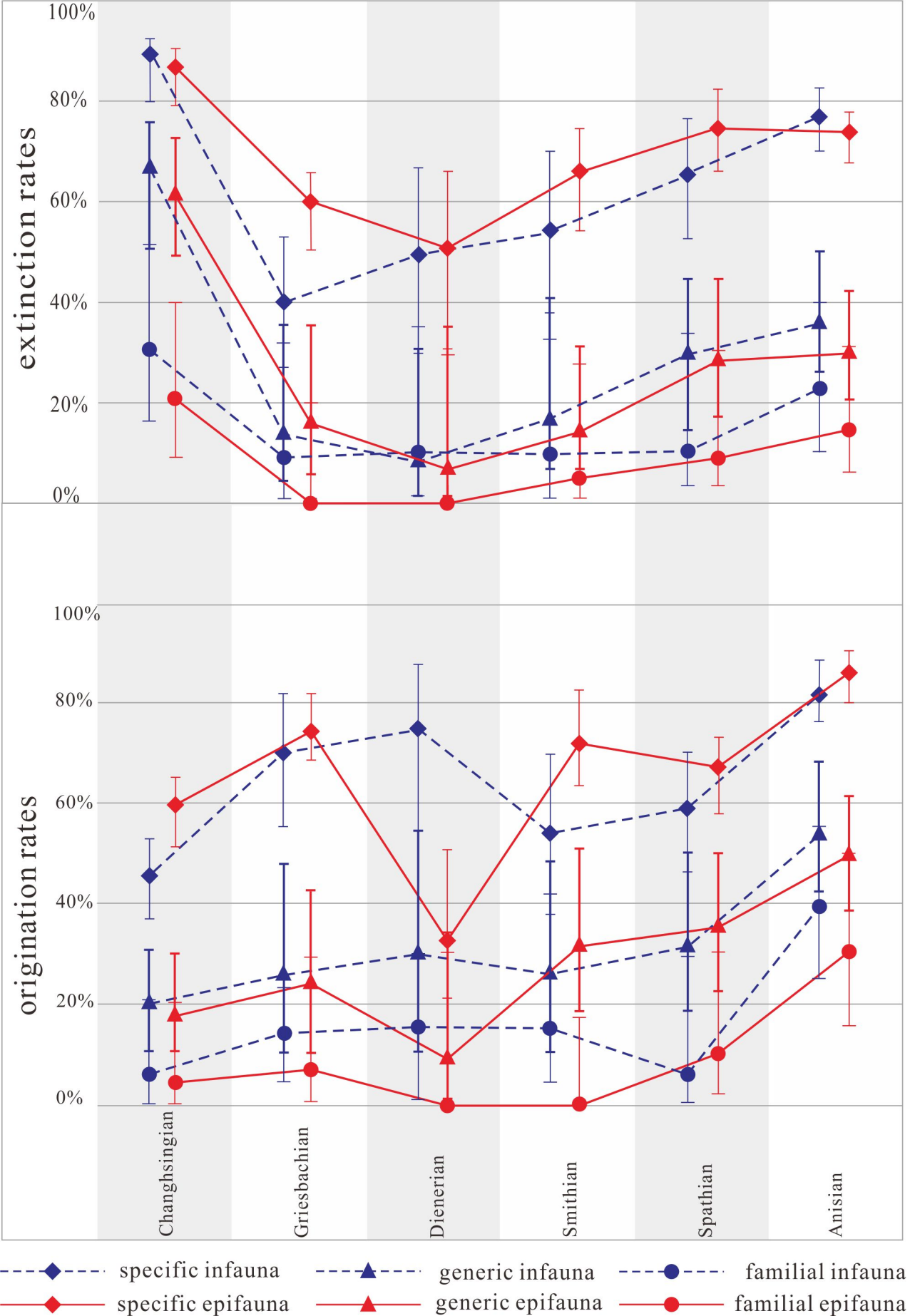
0

Genera

Family

Changhsingian
Griesbachian
Dienerian
Smithian
Spathian
Anisian

mobile infauna
stationary epifauna
mobile semi-infauna
slow-moving infauna
stationary low-level epifauna


extinction rates
100%
80%
60%
40%
20%
0%
origination rates
100%
80%
60%
40%
20%
0%
Changhsingian
Griesbachian
Dienerian
Smithian
Spathian
Anisian
specific infauna
generic infauna
familial infauna
specific epifauna
generic epifauna
familial epifauna

Intervals	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	314/197	76/23	15/2	85	64	32	54	19	4
Griesb.	85/121	7/11	0/4	53	16	0	75	27	15
Diene.	34/26	5/6	4/2	68	19	19	52	19	10
Smithian	70/74	7/13	2/2	61	16	7	65	30	7
Spathian	136/107	22/24	6/3	79	30	17	62	33	8
Anisian	318/351	45/64	11/21	75	37	20	83	52	37

Infaunal	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
Intervals	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	120/62	33/10	7/1	87	65	32	45	20	5
Griesba.	17/31	3/5	1/2	39	15	8	70	25	15
Diene.	11/17	1/4	1/2	48	7	8	74	29	17
Smithian	19/19	3/4	1/2	54	18	8	54	24	16
Spathian	41/37	8/10	2/7	65	27	12	59	33	6
Anisian	129/137	21/31	7/12	77	37	23	82	54	39

Epifaunal	Numbers of extin./new taxa			Proportional extinction rates(%)			Proportional origination rates(%)		
Intervals	Species	Genera	Family	Species	Genera	Family	Species	Genera	Family
Changhs.	181/126	35/11	5/1	85	61	21	59	19	4
Griesba.	68/89	4/6	0/1	58	16	0	75	24	6
Diene.	13/9	1/1	0/0	48	8	0	33	8	0
Smithian	51/58	4/9	1/0	65	15	6	73	33	0
Spathian	82/72	12/15	2/2	75	29	10	66	36	10
Anisian	186/215	20/32	4/8	73	31	15	85	50	30